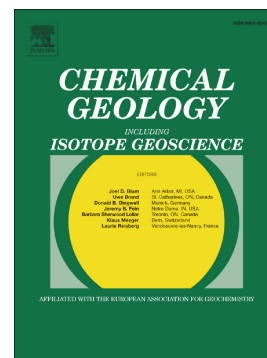


Accepted Manuscript

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PII: S0009-2541(17)30669-1
DOI: doi:[10.1016/j.chemgeo.2017.11.038](https://doi.org/10.1016/j.chemgeo.2017.11.038)
Reference: CHEMGE 18566
To appear in: *Chemical Geology*
Received date: 28 July 2017
Revised date: 2 November 2017
Accepted date: 27 November 2017

Please cite this article as: Siobhan Williams, Jochen Halfar, Thomas Zack, Steffen Hetzinger, Martin Blicher, Thomas Juul-Pedersen, Comparison of climate signals obtained from encrusting and free-living rhodolith coralline algae. The address for the corresponding author was captured as affiliation for all authors. Please check if appropriate. Chemge(2017), doi:[10.1016/j.chemgeo.2017.11.038](https://doi.org/10.1016/j.chemgeo.2017.11.038)

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Comparison of climate signals obtained from encrusting and free-living rhodolith coralline algae

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Abstract

Coralline algae have been used for sclerochronological studies throughout the last decade. These studies have focused on two different growth morphologies of the photosynthetic coralline algae: massive crusts forming small buildups on hard substrate, and free-living branching algal nodules, known as rhodoliths. The latter are generally found on soft-substrate, where they are frequently overturned by water movement and bottom feeding organisms, leaving one side of the rhodolith partially buried in the sediment at any given time. Here we test whether either of these growth morphologies is more suitable for proxy reconstructions by comparing Mg/Ca ratios – a temperature proxy – in multiple replicates of rhodoliths of *Lithothamnion glaciale* and in rhodoliths as well as encrusting specimens of *Clathromorphum compactum*. With both species being widespread throughout the Temperate and Arctic regions, we have chosen two North Atlantic localities at Nuuk Fjord, Greenland (Subarctic), and off the southeastern coast of Newfoundland, Canada (Temperate), for this study. Two to three Mg/Ca ratio transects spanning 18 years of growth were analysed on multiple specimens with encrusting morphologies and along different sides of rhodoliths using laser ablation inductively coupled mass spectrometry and compared to remotely sensed sea surface temperature (SST) data. The length of the common time span used for comparison was limited by growth interruptions in rhodoliths. Furthermore, our comparison is based on the assumption that rhodolith growth increments are annual – an assumption that has recently been challenged by mesocosm studies. Monthly Mg/Ca values from multiple transects within each individual were compared and in samples from Nuuk fjord significant correlations were found in 4 of 4 encrusting *C. compactum*, 4 of 4 *C. compactum* rhodoliths, and 2 of 3 *L. glaciale* rhodoliths. In Newfoundland significant correlations were found in 6 of 6 encrusting *C. compactum* comparisons (average: $r=0.61$, $p<0.001$), and in 6 of 6 *L. glaciale* rhodolith comparisons (average: $r=0.43$, $p<0.001$) for monthly resolved time series. The monthly Mg/Ca ratios ($n=216$) from each morphology were compared with instrumental Reynolds SST yielding the following correlations: encrusting *C. compactum* ($r=0.64$, $p<0.001$), *C. compactum* rhodolith ($r=0.62$, $p<0.001$) and *L. glaciale* ($r=0.58$, $p<0.001$). In Newfoundland both morphologies indicate a similar strength in recording SST: encrusting *C. compactum* ($r=0.85$, $p<0.001$) and rhodolith-forming *L. glaciale* ($r=0.84$, $p<0.001$). In summary, Mg/Ca ratios derived from both coralline algal growth forms can yield SST information, however, massive encrusting forms generally yield higher correlations to SST than transects measured on individual rhodoliths, which only allowed for the generation of short uninterrupted time series due to frequent growth irregularities.

Highlights

- Comparison of encrusting and rhodolith coralline algae for paleoclimate reconstruction
- Both coralline algal forms can yield SST information, but encrusting forms generally yield higher correlations to SST

- Encrusting morphologies yielded longer records due to frequent growth irregularities in rhodoliths

Key Words

Red coralline algae

Sclerochronology

Abbreviations

SST – Sea surface temperature

MODIS - Moderate Resolution Imaging Spectroradiometer

LA-ICP-MS – Laser ablation inductively coupled mass spectrometry

Funding: This work was funded by the Centre for Global Change Science; the American Geophysical Union; and an NSERC Discovery grant to JH.

Declaration of interest

The authors declare no competing interests.

1. Introduction

Accurate instrumental sea surface temperature (SST) data only extends back to the 1850's and only in a select few places (Rayner et al., 2003), while in more remote locations data exist only for the last few decades. This leaves a significant gap in our knowledge of past climate, especially in poorly studied regions such as the Subarctic and Arctic. In these regions proxy data are required to provide extended time series of past climate. A better understanding of past climate decreases the uncertainty of projections of future climate through models. Typically, annual and subannual resolution environmental proxy data from high-latitude terrestrial settings have come from tree rings, lake sediments and ice cores that can provide information about temperatures and rainfall over centuries and millennia (Fritts and Swetnam, 1989). In temperate to subarctic oceans bivalve shells have been used to reconstruct environmental conditions including surface temperatures (e.g. Butler et al., 2010; Reynolds et al., 2013; Schöne et al., 2005), and coralline algae from subarctic and arctic settings have served as a proxy for temperature as well as a variety of environmental variables such as light, glacial runoff, nutrients, freshwater and sea ice variability (Burdett et al., 2012; Chan et al., 2017; Halfar et al., 2013; Hetzinger et al., 2013; Kamenos et al., 2012). Extratropical climate reconstructions from the annual-increment forming photosynthetic coralline algae have focused on two different growth morphologies and genera: massive crusts of *Clathromorphum compactum* and *Clathromorphum nereostratum* forming buildups as thick as 50 cm on hard substrate (Adey et al., 2013; Chenelot et al., 2011), and free-living branching algal nodules, so called rhodoliths, of the species *Lithothamnion glaciale* (Kamenos et al., 2013).

While *C. compactum* commonly occurs as encrusting small buildups that have a hemispherical shape with a smooth surface (Adey, 1965), it has recently also been found in the form of free-living massive (i.e. non-branching) rhodolith nodules (Jørgensbye and Halfar, 2016). Individual specimens of encrusting *C. compactum* can have lifespans of up to 650 years with maximum annual growth rates of 400µm/year (Halfar et al., 2013). Annual growth rates do not exhibit a decline with

increasing specimen age (ontogenetic decline) allowing the use of annual growth as a paleoclimate proxy without requiring the statistical removal of ontogenetic trends (Halfar et al., 2008). Removal of ontogenetic trends has been shown to obscure long-term climate variability (Schöne et al., 2005). *C. compactum* is widely-distributed throughout the Arctic and Subarctic, with often dense coverage on rocky substrate at water depths ranging from 5-30m and has been sampled as far north as 79.5° (J. Halfar, pers. obs.).

L. glaciale exhibits a branching morphology and can grow attached or unattached (Figure 1). *L. glaciale* lives in the mid to lower photic zone and occasionally in tide pools and the upper photic zone (Adey, 1970). Although its growth is not inhibited at high light levels, branches are too fragile to withstand heavy wave action (Adey, 1970). Compared to other species of sub-arctic coralline algae *L. glaciale* is relatively fast growing, up to ~12µm/day in optimal conditions (Adey, 1970). As a result it is the most abundant coralline species in the North Atlantic (Adey, 1970).

Rhodolith-forming morphologies of *L. glaciale* and *C. compactum* are generally found on soft-substrate, where they are overturned by water movement and bottom feeding organisms, leaving one side of the rhodolith partially buried in the sediment at any given time (Marrack, 1999). Rhodolith turning frequency can also be correlated with water depth, since rhodoliths are turned by waves, rather than tidal currents, so shallow rhodoliths are more frequently moved (Steller and Foster, 1995). Depending on the environmental setting it is possible that rhodoliths are not moved on a regular schedule and that the side facing the seafloor, which is often partially buried in sandy sediment, may cease growing if it remains buried for too long (Freiwald and Henrich, 1994).

In this study, we evaluate the climate archiving potential of both genera by comparing Mg/Ca ratio-based time series from samples collected at two North Atlantic localities: (1) Massive growing *C. compactum* rhodoliths and encrusting samples, as well as *L. glaciale* rhodoliths from Nuuk, Greenland, and (2) encrusting

C. compactum and *L. glaciale* rhodoliths from Bay Bulls, Newfoundland (Figure 2). At both localities we will statistically test for inter- and intra-specimen time-series similarities, as well as compare algal Mg/Ca ratios with local instrumental temperature time series.

2. Methods

2.1 Sampling

Coralline algae were live collected in the Nuuk fjord in Greenland (64°10 N, -51°60 W; 12 m depth) by dredge (rhodoliths) or by divers (encrusting morphologies) in summer 2013. Rhodoliths and encrusting coralline algae were also collected near Saint John's, Newfoundland (47°18 N, 52°47 W; 9 m depth) by divers in summer 2008 (Table 1). Live collection of *C. compactum* was determined by the presence of an undamaged meristem (sub-surface growth plate) and an epithallial crust (cover cells), which is extremely fragile and is easily dislodged after death. In addition, live collection of branched *L. glaciale* rhodoliths was confirmed by the presence of pink pigmentation on all branches. Encrusting samples were selected based on maximum thickness, while the most spherical rhodolith samples were chosen. *C. compactum* rhodoliths selected for this project all contained a pebble nucleus, *L. glaciale* did not have nuclei (see Figure 1). From the Greenland collection 4 of 13 encrusting *C. compactum* samples, 5 of 14 *C. compactum* rhodoliths, and 3 of 3 *L. glaciale* rhodoliths were analysed. From the Newfoundland collection 4 of 14 encrusting *C. compactum* samples, and 4 of 7 *L. glaciale* rhodoliths were analysed.

2.2 Sample preparation

Due to the fragility of the fine branches (average branch thickness 3 mm), *L. glaciale* samples were embedded in resin prior to preparation. All samples were thick sectioned and polished to 1µm. The software geo.TS (Olympus Soft Imaging Systems) was utilized with an automated sampling stage on a reflected light microscope to produce two-dimensional maps of the polished samples (for details see Hetzinger et al., 2009). These high-resolution composite images were used to count growth increments, and to select the most promising long-lived individuals in

terms of regularity of growth increments and length of a continuous record for geochemical analysis.

2.3 Analysis

Mg/Ca ratios of coralline algae were measured with laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) along line profiles. Data obtained with this method formed the basis for generating annual resolution age models. Mg/Ca ratios have previously been used as a paleotemperature proxy in coralline algae (e.g. Hetzinger et al., 2011, Kamenos et al., 2009; Williams et al., 2014). Each sample underwent a pre-ablation step to remove surface contaminants, and line transects were programmed to avoid unconformities and conceptacles. A New Wave NWR 213 laser ablation system coupled with an Agilent 8800 Quadrupole ICP-MS in the Earth Sciences department at Gothenburg University were used to measure ^{24}Mg , and ^{43}Ca . For these measurements laser energy was approximately 6 J/cm^2 , helium and nitrogen were carrier gases. The laser spot used was a $50 \text{ }\mu\text{m}^2$ square and traveling speed of the sampling stage was set at $10 \text{ }\mu\text{m/second}$ with a 10Hz pulse rate. The internal standard was ^{43}Ca , using calcium concentrations measured by ICP-OES (Hetzinger et al., 2009). The external standard was NIST SRM 610 glass (US National Institute of Standard and Technology Standard Reference Material). Periodic measurements of NIST SRM 610 were taken to quantify instrumental drift. GLITTER 4.4.4 (Macquarie University, Sydney) was used for data reduction.

Two to three LA-ICP-MS transects were analysed on each sample along the direction of growth from young to old to generate an at least 18 year long time series (Greenland: 2012-1994, Newfoundland: 2008-1990). These years were established by assigning the year of live collection to the most recent band and counting back. Eighteen years was the longest common time span that could be analyzed in all samples without a detectable unconformity (irregularity or interruption in growth). No analyses were performed beyond any unconformity. Unconformities were common in rhodoliths, while the encrusting specimens would have allowed for

generating significantly longer time series. On the encrusting samples the transects were parallel to one another. On the rhodoliths lines were analysed on different sides, and in the case of the branching *L. glaciale* specimens, transects followed the center of the branch axis as much as possible (Figure 1).

It was assumed that growth increments of all morphologies were annual, and this annual cyclicity of Mg/Ca ratios was used to create age models, where the annual minimum Mg/Ca value was marked as representing January and the maximum was marked as August as these months have the coolest and warmest temperatures annually at the study sites. Age models were verified by overlaying Mg/Ca time series graphs onto high-resolution images of the polished samples. The program AnalySeries 2.0.8 (Paillard et al., 1996) was used to resample the Mg/Ca time series to yield monthly resolution Mg/Ca data.

Using IBM SPSS Statistics for Macintosh (Version 22) multiple linear regressions of Mg/Ca ratios from three transects on each specimen were compared to evaluate intra-specimen variability. This type of analysis was used to explain the relationship between three or more variables. Next, the data from all transects on each sample were averaged and these averages were compared to all other samples from the same location to test the strength of their common signal. Finally, Mg/Ca time series from rhodoliths and encrusting specimens were compared to in situ instrumental and remotely sensed satellite temperature data obtained for the collection sites.

2.4 Instrumental data

Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua SST data (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, n.d.) was used to compare local temperatures to algal Mg/Ca data. In Nuuk a single grid point (1 by 1 km) was chosen (2002-2011; Lon=-51.53°E; Lat=60.07°N), but in the small embayment of Bay Bulls selecting a larger spatial grid of (3 by 3 km) was required to reduce the number of points with no data (2002-2007; Lon=-52.6987 – -52.6637°E; Lat=47.2695 – 47.3031°N). In addition, Reynolds sea surface temperature

reanalysis data were calculated from 5°x5° squares (~425 by 555 km) in Nuuk (1994-2012; Lon=-57 – -55°E; Lat=59 – 64°N)(Reynolds et al., 2002) and the Bay Bulls location (1990-2007; Lon=-55 – -50°E; Lat=47 – 52°N) for comparison with corresponding Mg/Ca. The MODIS data covers fewer years, but provides temperature data at high spatial resolution, while Reynolds data covers the entire study period and is calculated from satellite data, but uses a larger grid size than MODIS. Finally, seven years (2012-2002) of in situ temperature data from 7 m depth in Nuuk fjord, collected by the Greenland Institute of Natural Resources using a Sea-Bird Electronics SBE 19plus SEACAT Profiler CTD (conductivity, temperature and depth), were compared to the MODIS SST to test the difference between depth of collection and SST, as well as the difference between remotely sensed and in situ temperature data (Figure 3). The correlation between the two was significant ($n=74$, $r=0.77$, $p<0.001$) but summer peaks were warmer at the surface than at 7m. Given the high correlation between in situ and remotely sensed temperatures, and the longer time span of the MODIS data, only MODIS temperatures were used. P-values adjusted for autocorrelation (the similarity between a time series and a lagged version of itself, in this case driven by the seasonality of temperature) were not reported in the results because they were the same as p-values prior to adjustment.

3. Results

3.1 Greenland:

A comparison of monthly values of individual transects within each sample showed variability between transects (Figures 4-6), but significant correlations were found in 4 of 4 encrusting *C. compactum*, average: ($n=216$, $r=0.34$, $p<0.001$), 4 of 5 *C. compactum* rhodoliths, average: ($n=216$, $r=0.33$, $p<0.001$), and 2 of 3 *L. glaciale* rhodoliths, average: ($n=216$, $r=0.42$, $p<0.001$). In most cases, the annual cycles showed clear differences between the summer highs and winter lows, but these cycles also contained many variations between the Mg/Ca values reached at summer highs and winter lows of individual transects. For example, in Figure 5a from 1995-1998 is a period when summer highs and winter lows align well, and 2000-2003 is a period when highs and lows do not match. Typically, in samples

containing three transects, regardless of coralline type, the highs and lows of two transects never aligned well throughout the entire series; instead portions of the series lined up between the various transects, while other portions did not (Figures 4-6). When comparing transects it becomes evident that single years in some transects are occasionally not recorded consistently (Figure 6).

The averaged monthly Mg/Ca time series from each specimen of the same morphology were compared to the other individuals from the same morphology (Figures 4-6). Using multiple regression analysis, significant correlations existed in all three morphologies: encrusting *C. compactum* ($n=216$, $r=0.56$, $p<0.001$), *C. compactum* rhodoliths ($n=216$, $r=0.64$, $p<0.001$), and *L. glaciale* rhodoliths ($n=216$, $r=0.63$, $p<0.001$). These series had less intra-annual variability than the individual transect series since they were averaged, but still show greater variability between the Mg/Ca values reached at both the summer highs and the winter lows within their annual cycles (Figures 4-6).

All monthly Mg/Ca time series from each of the three types of coralline algae were averaged and correlated with 9 years of monthly MODIS SST from Nuuk Fjord (2003-2012). All encrusting *C. compactum* ($n=108$, $r=0.5$, $p<0.001$), *C. compactum* rhodolith ($n=108$, $r=0.61$, $p<0.001$) and *L. glaciale* ($n=108$, $r=0.57$, $p<0.001$) records correlated significantly to SST. Similarly, when compared to Reynolds SST, which covers the 18 years of our series (1994-2012), all of the coralline morphologies correlated significantly: the encrusting *C. compactum* ($r=0.64$, $p<0.001$, Figure 8), *C. compactum* rhodolith ($r=0.62$, $p<0.001$; Figure 8) and *L. glaciale* ($r=0.58$, $p<0.001$; Figure 8). Finally, seasonally averaged (March-August) Mg/Ca ratios for each coralline algae morphology were compared to seasonal (March-August) Reynolds SST. None of the records correlated significantly: while encrusting *C. compactum* Mg/Ca values exhibited a positive temperature relationship ($n=18$, $r=0.35$, $p=0.07$), both the *C. compactum* ($n=18$, $r=-0.31$, $p=0.10$) and the *L. glaciale* rhodoliths ($n=18$, $r=-0.04$, $p=0.44$) exhibited negative relationships (Figure 9). The comparison of summer peaks (Aug/Sept) between coralline Mg/Ca and SST also did not yield

significant relationships. When compared with MODIS SST (Aug/Sept) the correlations were not significant or negative (encrusting *C. compactum* (n=10, $r=0.27$, $p=0.23$), *C. compactum* rhodolith (n=10, $r=-0.49$, $p=0.08$) and *L. glaciale* (n=10, $r=0.12$, $p=0.37$)). Similarly, when compared with Reynolds SST (Aug/Sept) correlations were not significant or negative: encrusting *C. compactum* (n=18, $r=0.05$, $p=0.42$), *C. compactum* rhodolith (n=18, $r=-0.58$, $p=0.006$), and *L. glaciale* (n=18, $r=-0.4$, $p=0.05$).

3.2 Newfoundland:

Monthly values from multiple transects within each individual were compared using multiple linear regressions and significant correlations were found in 4 of 4 encrusting *C. compactum* individuals (average n=216, $r=0.62$, $p<0.001$; Figure 10) and in 4 of 4 *L. glaciale* rhodoliths (average n=216, $r=0.43$, $p<0.001$; Figure 11). Both *C. compactum* and *L. glaciale* had clear annual cycles despite variability within them, similar to the samples collected from Greenland. In general, the encrusting samples displayed less intra-annual variability than rhodoliths (Figures 9 and 14).

Three transects from each sample's monthly Mg/Ca ratios were averaged to create a single specimen time series. The averaged time series were compared with other samples of the same algal morphologies. Significant correlations using multiple linear regression were found between all encrusting *C. compactum* samples (n=216, $r=0.61$, $p<0.001$) and all *L. glaciale* rhodoliths (n=216, $r=0.73$, $p<0.001$). Despite overall correlations being strong, there were inter-sample differences during selected time intervals (e.g. in year 1995 in Figure 11).

Finally, averaged monthly transects from each of the two types of coralline algae were compared to MODIS SST (2002-2008) and yielded the following relationship for *C. compactum*: n=72, $r=0.84$, $p<0.001$, and for *L. glaciale* n=72, $r=0.87$, $p<0.001$ (Figure 13). Also, both the encrusting morphologies (n=216, $r=0.85$, $p<0.001$; Figure 12) and rhodoliths (n=216, $r=0.84$, $p<0.001$; Figure 12) correlated significantly with Reynolds SST (18 years) (Figure 13). Seasonally averaged (March-August) Mg/Ca of

each coralline algae morphology (inter-sample) were compared to seasonally averaged (March-August) Reynolds SST, and neither of the records correlated significantly: encrusting *C. compactum* ($n=18$, $r=0.37$, $p=0.06$), and *L. glaciale* rhodoliths ($n=18$, $r=0.37$, $p=0.06$) (Figure 14). When the Mg/Ca ratios of each specimen and Reynolds SST (March-August) were correlated all of the rhodoliths had weaker correlations than the inter-sample average, and three of the four encrusting morphologies had weaker correlations than the average (Table 2). The comparison of summer peaks (Aug/Sept) between coralline Mg/Ca and SST also did not yield significant relationships. When compared with MODIS SST (Aug/Sept) the correlations were: *C. compactum* ($n=6$, $r=0.28$, $p=0.29$) and *L. glaciale* ($n=6$, $r=0.41$, $p=0.21$). When compared with Reynolds SST (Aug/Sept) correlations were not significant with *C. compactum* ($n=18$, $r=0.16$, $p=0.26$) and significant with *L. glaciale* ($n=18$, $r=0.63$, $p=0.002$).

4. Discussion

Statistically the strength of intra- and inter- sample correlations were similar between morphologies, but while the monthly temperature vs. Mg/Ca relationships of each morphology were significant, the relationship was stronger in Newfoundland than in Nuuk fjord. All samples include Mg/Ca series where the high and lows align well between the individual transects, and time series where they do not. The best explanation for these differences could be the result of variable growth caused by natural phenomena such as differential shading due to temporary macroalgal overgrowth, small scale disturbance due to bioerosion (e.g. urchin grazing), or unidentified branch breakage in the case of finely branching *L. glaciale*. In addition, age model errors could have been introduced due to the misidentification of annual growth increments. Also, conceptacle cavities (uncalcified reproductive structures; Figure 1) and surrounding calcite exhibit Mg/Ca values that are not reflective of temperature and must be avoided during analysis. Since conceptacles are found throughout the *C. compactum* specimens they can be buried just below the polished surface. Hence, laser ablation transects on occasion might sample calcite surrounding conceptacle cavities and would therefore

yield Mg/Ca signals that do not represent temperatures. This does not apply to *L. glaciale* as its conceptacles are located on the margins of branches, while laser ablation measurements took place along branch centers (Figure 1). Urchin grazing of both encrusting and rhodolith *C. compactum* can cause a partial or complete removal of growth increments and therefore temperature information. This partial removal can result in the elimination of summer or winter Mg/Ca extremes, reducing the amplitude of the annual temperature signal. When the amount of tissue removed is small, the missing portion can go visually unnoticed. However, careful analysis of polished sections prior to analysis can often identify grazed regions, so that they can be avoided. Urchin grazing does not typically affect finely branched rhodoliths, so grazing-related damage does not occur in *L. glaciale* (Vance, 1979). However, *L. glaciale* is prone to breakage of the fragile branches that can be succeeded by regrowth (Pueschel and Keats, 1997). This may be difficult to detect, as the area of unconformity would be relatively small compared to that of a non-branching morphology.

Despite the intra- and inter- sample variability linear regressions between each morphology and Reynolds SST showed a similar relationship within each geographical region:

Encrusting *C. compactum* (Greenland): $\text{Mg/Ca} = 0.0017 \text{ temperature } [^{\circ}\text{C}] + 0.064$ ($R^2=0.41$, standard error of slope=0.0001, standard error of y-intercept=0.0006)
When two instrumental temperature outliers in Figure 8 (August and September 2010) are not included the relationship changes to: $\text{Mg/Ca} = 0.0017 \text{ temperature } [^{\circ}\text{C}] + 0.064$ ($R^2=0.37$)

Rhodolith *C. compactum* (Greenland): $\text{Mg/Ca} = 0.0017 \text{ temperature } [^{\circ}\text{C}] + 0.064$ ($R^2=0.39$, standard error of slope=0.0001, standard error of y-intercept=0.0006)
When two instrumental temperature outliers in Figure 8 (August and September 2010) are not included the relationship changes to: $\text{Mg/Ca} = 0.0018 \text{ temperature } [^{\circ}\text{C}] + 0.064$ ($R^2=0.38$)

Rhodolith *L. glaciale* (Greenland): $\text{Mg/Ca} = 0.002 \text{ temperature } [^{\circ}\text{C}] + 0.067$
 $(R^2=0.34, \text{ standard error of slope}=0.0002, \text{ standard error of y-intercept}=0.0008)$
 When two instrumental temperature outliers in Figure 8 (August and September 2010) are not included the relationship changes to: $\text{Mg/Ca} = 0.0021 \text{ temperature } [^{\circ}\text{C}] + 0.066$ ($R^2=0.34$)

There is a significant difference between all three slopes ($p>0.001$).

Encrusting *C. compactum* (Newfoundland): $\text{Mg/Ca} = 0.0018 \text{ temperature } [^{\circ}\text{C}] + 0.072$
 $(R^2=0.72, \text{ standard error of slope}=0.00008, \text{ standard error of y-intercept}=0.0005)$

Rhodolith *L. glaciale* (Newfoundland): $\text{Mg/Ca} = 0.0018 \text{ temperature } [^{\circ}\text{C}] + 0.080$
 $(R^2=0.70, \text{ standard error of slope}=0.00008, \text{ standard error of y-intercept}=0.0005)$

There is no significant difference between slopes ($t=0.34, p=0.73$).

Comparing the relationships between Mg/Ca and temperature of Greenland *C. compactum* samples to Newfoundland *C. compactum* and *L. glaciale*, the slopes are similar, but the y-intercepts of the Newfoundland samples are 0.01 higher. This results in the same Mg/Ca ratio corresponding to a higher temperature in Greenland samples than in Newfoundland samples. Several different MgCO_3 [mol %] to temperature relationships have been established for coralline algae, and similar to this result, they are both species and site specific. *L. glaciale* rhodoliths collected from the Strait of Belle Isle, Newfoundland exhibit a slope of 0.62 (after conversion to Mg/Ca [$\mu\text{g/g}$])(Halfar et al., 2000), two records from encrusting *Clathromorphum nereostratum* collected in the Aleutian Islands exhibit a slope of 2.3 (after

conversion to Mg/Ca [$\mu\text{g/g}$])(Hetzinger et al., 2009) and a slope of 0.007 (after conversion to Mg/Ca [$\mu\text{g/g}$])(Williams et al., 2014), and *L. glaciale* rhodoliths collected in Scotland exhibit a slope of 0.81 (after conversion to Mg/Ca [$\mu\text{g/g}$])(Kamenos et al., 2008). The calibrations in this study show Mg/Ca to be less sensitive to changes in SST (i.e. our linear regressions have a less steep slope) than the Hetzinger et al. (2011) calibration of encrusting *C. compactum* also collected in Newfoundland, or the Kamenos et al. (2008) calibration of *L. glaciale* collected in Scotland. However, the Mg/Ca sensitivity in this study (regression slopes of 0.0017-0.002) was similar to that found in a study which analysed coralline algae from nine North Atlantic locations (regression slope of 0.002)(Nash and Adey, 2017).

The correlations between Mg/Ca and SST were stronger in Newfoundland than in Nuuk, likely indicating the influence of another factor such as glacial runoff or light influencing Mg/Ca in addition to temperature at the Nuuk site. Also, Reynolds SST is an interpolated data set, which means that the uncertainty of a data point is unknown (Foody and Atkinson, 2002). In situ data from Greenland correlated significantly with Reynolds SST ($r=0.88$, $p<0.001$), but without a perfect correlation it is possible that periods of weak correlation between the coralline algae and SST may be a result of SST differing from the in situ temperatures. The fjord setting where the Nuuk samples were collected is influenced by glacial runoff. As a result, the surface layer is characterized by higher temperatures and lower salinities than the subsurface waters in the summer as a result of freshwater runoff from land and precipitation (Mortensen et al., 2011). Temperature and salinity vary within the fjord depending on distance from sources of freshwater, including precipitation, river outflow, and glacial melt from icebergs and glacier termini (Mortensen et al., 2013). Meanwhile, Bay Bulls Newfoundland has no large rivers emptying into it and surface temperature distribution is uniform. The mixing between the glacial runoff and seawater in Nuuk fjord, may be a cause of the lower correlations between SST and Greenland coralline Mg/Ca, or possibly weaker correlations between SST and temperature at the depth of coralline collection since SST are more susceptible to factors such as runoff, stratification, and daily heating (Campagna et al., 2000).

Despite this difficulty, Nuuk fjord is the only location known to date where both encrusting and rhodolith *C. compactum* have been found co-occurring thus allowing a direct comparison of the two morphologies.

The importance of light for growth in different genera of coralline algae has long been demonstrated by Moberly (1968). Teichert and Freiwald (2014) also found light to be the most important, and mean annual temperature to be the second most important physical parameter limiting the calcium carbonate production of coralline algae on the Svalbard shelf (Teichert and Freiwald, 2014). The correlation between light and growth has allowed the use of *C. compactum* as a proxy for reconstructing sea ice variability because sea ice blocks light from reaching the coralline algae living below and causes growth rates to slow (Halfar et al., 2013). This highlights the potential importance of shading on the substrate facing side of rhodoliths as a cause of differences between different directions of branch orientation in a single rhodoliths (see discussion below).

When developing a climate proxy, only the climate factors are of interest while non-climate factors detract from the record and they are removed or minimized by averaging of multiple samples (Cook and Kairiukstis, 1990). This is because the non-common variability (noise) can be reduced through averaging the replicate series. This common signal represents the common forcing on the tree-rings (Briffa, 1999) and is what we are attempting to produce for each type of coralline. This explains why, in all of our comparisons the correlations between records were improved as transects were averaged within individuals, and individuals were averaged within morphologies, as was shown by earlier studies of coralline algae (Halfar et al., 2011; Hetzinger et al., 2018; Wanamaker et al., 2011). Averaging is also a common practice with other proxies, such as tree-rings (Fritts and Swetnam, 1989). The differences in parts of an individual coralline or differences between individuals are likely due to the various environmental factors listed above, and in the case of rhodoliths, turning resulting in half of the rhodolith being shaded at any given point in time (Figure 15). Since the timing of rhodolith turning is random it is unlikely that growth and Mg/Ca

incorporation on all sides will provide a complete record of environmental conditions on any given side. The side facing the seafloor, which is often partially buried in sandy sediment, may cease growing or be incorporating a different Mg/Ca ratio than the light facing side (Figure 15). In fact, short term burial can also slow the growth without cessation causing a distortion of the record (Freiwald and Henrich, 1994). While rhodoliths have been used for climate reconstructions (Kamenos, 2010), a mesocosm study of Panamanian *Lithothamnion* sp. has suggested that growth increment widths and Mg/Ca ratios are unrelated to temperature in this study (Sletten et al., 2017a, 2017b). Hence, growth irregularities related to rhodolith turning and temporary partial burial are possibly the cause of weak or insignificant (e.g. negative) correlations in rhodoliths compared to encrusting specimens. Additionally, uneven light receipt by individual branches caused by rhodolith turning may explain the differing Mg/Ca to temperature calibrations between species from the same sites (Figure 14).

There has been conflicting evidence with respect to the annual character of rhodolith growth increments. Freiwald and Henrich (1994) were the first to demonstrate the existence of two tiers of banding – an annual and a subannual banding pattern – in *L. glaciale* from Norway. This was later confirmed by electron microprobe mapping of Newfoundland collected specimens of *L. glaciale* (Halfar et al. 2000). In contrast, the annual nature of rhodolith growth increments has been tested in *L. glaciale* rhodoliths using specimens reared in the wild, and rhodoliths stored in flow-through tanks for 12 months, in Scotland, where increments were determined to be annual (Kamenos et al., 2008). Yet in the Panamanian mesocosm study of *Lithothamnion* sp. growth increments were sub-annual and the number of increments formed in a given time-span were highly inconsistent between individuals (Sletten et al., 2017a). This suggests that the rate of increment formation in rhodoliths should be confirmed regionally before assuming annual formation. The non-annual character of growth increments could possibly be the cause of non-significant and negative annual Mg/Ca – SST relationships in Greenland rhodoliths, while Newfoundland rhodoliths, which yielded significant Mg/Ca – SST

relationships, might exhibit annual increments only. While *Lithothamnion* growth increment periodicity appears to be variable, multiple lines of evidence have confirmed the annual character of growth increments of encrusting *Clathromorphum* sp.: (A) Growth increment counts could be matched with U/Th and radiocarbon ages in live collected specimens from the North Pacific and northwestern Atlantic (Halfar et al., 2007, 2013), (B) A one year calibration study in the wild produced annual growth increments in multiple specimens (Halfar et al. 2008), and (C) conceptacles, which are produced annually in *C. nereostratum* are consistently initiated within a single increment. No tests confirming the annual character of *C. compactum* rhodoliths have been undertaken to date.

It should also be noted, that perhaps a greater rhodolith selection, allowing for the analysis of more spherical rhodoliths could improve the results. The shape of each rhodolith is likely determined by bottom organisms and hydrodynamics, and can indicate their ease of transport, e.g. spherical rhodoliths with equal growth on all sides are less resistant to turning and transport (Steneck, 1986). Therefore, rhodoliths with even growth on all sides (roughly spherical) are more likely to have turned frequently and would perhaps yield a better record than specimens with uneven crust thickness. Also, dense or thick branches in branching coralline algae suggests they grew in a more energetic environment (Marrack, 1999) where they have turned more frequently. However, in an energetic environment rhodolith branches are also subject to more frequent breakage. Indicators of frequent turning may then suggest that Mg/Ca was incorporated evenly on all sides and would therefore produce a more accurate temperature record.

5. Conclusions

In conclusion, according to the data presented here both morphologies of coralline algae produce similarly accurate temperature reconstructions in some regions, such as the Newfoundland collection site, while at the Greenland site the encrusting morphologies produced better temperature records than either rhodolith species. This could be due the fact that rhodolith growth increment formation is not

necessarily annual at some locations and may therefore lead to the generation of erroneous age models. Rhodoliths can be effectively collected by dredge, but encrusting coralline algae must be collected by divers or submersible, meaning that rhodoliths are a more accessible archive, especially for short-term (e.g. decadal) records from individual plants. Meanwhile, the recorded uninterrupted lifespan of encrusting *C. compactum* samples is much longer, permitting continuous multicentury reconstructions from individual plants (Chan et al., 2017; Halfar et al., 2013; Williams et al., 2017). The record lengths were limited by the number of uninterrupted years of growth below the living surface found within the rhodolith samples. The longest record from a single encrusting coralline algae is 647 years (*C. compactum*) (Halfar et al., 2013) while individual *L. glaciale* rhodoliths have been found with ~70 years of growth (Kamenos et al., 2012). Regardless of the type of coralline algae chosen, however, this study, along with previous work (Williams et al. 2014; Hetzinger et al. 2018) stresses the importance of reducing the effect of biological variability by replication and averaging of data from multiple specimens in order to increase strength of climate signals.

Acknowledgements

We acknowledge the marine monitoring program MarineBasis-Nuuk, part of the Greenland Ecosystem Monitoring (GEM), for supplying the in-situ temperature data.

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Figure Captions

Figure 1. Cross-sections of *C. compactum* and *L. glaciale* showing position of LA-ICP-MS transects (*L. glaciale* rhodolith top left, *C. compactum* rhodolith top right, *C. compactum* encrusting bottom. Encrusting *C. compactum* specimen displays laser transects across 120 years of continuous growth, however only the youngest 18 were used in this study. Inset shows detail of annual growth increments and conceptacle cavities (uncalcified reproductive structures) in the encrusting *C. compactum* specimen.

Figure 2. Location of sample collection sites.

Figure 3. Monthly MODIS Aqua satellite SST data (NASA Goddard Space Flight Center, Ocean Ecology Laboratory, n.d.) from a single grid point (Lon=-51.53°E; Lat=60.07°N) compared to in situ temperature data from 7 m depth in Nuuk fjord, collected by the Greenland Institute of Natural Resources using a Sea-Bird Electronics SBE 19plus SEACAT Profiler CTD (conductivity, temperature and depth).

Figure 4. A) Monthly resolution Mg/Ca data from two transects analyzed on encrusting *C. compactum* specimen 5c, Nuuk, Greenland. B) Monthly resolution Mg/Ca time series of four encrusting *C. compactum* samples. Each time series represents monthly values averaged from 2 – 3 individual transects on a particular sample.

Figure 5. A) Monthly resolution *C. compactum* rhodolith Mg/Ca transects from specimen GR2RH09a, Nuuk, Greenland. B) Monthly resolution Mg/Ca time series of five *C. compactum* rhodolith samples. Time series from individual samples represent the averaged values of three transects measured. C) An example demonstrating well aligned Mg/Ca peaks during years 1995-1997 (from dashed rectangle in panel A). D) An example demonstrating are poorly aligned Mg/Ca peaks during years 2000-2002 (from dashed rectangle in panel A).

Figure 6. A) Monthly resolution *L. glaciale* rhodolith Mg/Ca transects from specimen GR5A, Nuuk, Greenland. B) Mg/Ca time series of three *L. glaciale* samples. Time series from individual samples represent the averaged values of three transects measured.

Figure 7. Mg/Ca time series of encrusting and rhodolith forming *C. compactum* and *L. glaciale* samples from Nuuk, Greenland. Time series from each group represent the averaged values of all transects from all samples (top) compared to monthly instrumental temperatures (bottom). A seawater temperature of -1.94°C is assigned to periods of ice cover in MODIS data.

Figure 8. Linear regression between 18-year time series of monthly Reynolds instrumental temperature data and Greenland encrusting *C. compactum* monthly Mg/Ca ratios (9 transects averaged from 4 samples), *C. compactum* rhodolith Mg/Ca (14 transects averaged from 5 samples), *L. glaciale* rhodolith Mg/Ca (9 transects averaged from 3 samples) and Reynolds temperature data over 18 years.

Figure 9. Annually-resolved Mg/Ca time series from encrusting and rhodolith forming *C. compactum* and *L. glaciale* samples from Nuuk, Greenland. Time series from each group represent the averaged values of all transects from all samples compared to annual instrumental temperatures. Reynolds SST correlated with encrusting *C. compactum* ($n=18$, $r=0.35$, $p=0.07$), *C. compactum* rhodolith ($n=18$, $r=-0.31$, $p=0.10$) and *L. glaciale* ($n=18$, $r=-0.04$, $p=0.44$).

Figure 10. A) Monthly resolution Mg/Ca data from two transects analyzed on the encrusting *C. compactum* specimen 08-SJ-21, Newfoundland, Canada. B) Monthly resolution Mg/Ca time series of four encrusting *C. compactum* samples. Each time series represents monthly results averaged from 2 – 3 individual transects on a particular sample.

Figure 11. A) Monthly resolution *L. glaciale* rhodolith Mg/Ca transects from specimen 08-SJ-RH2, Newfoundland, Canada. B) Mg/Ca time series of three *L. glaciale* samples. Time series from individual samples represent the averaged values of three transects measured. C) An example demonstrating poorly aligned Mg/Ca peaks during years 1990-1991 (from dashed rectangle in panel B).

Figure 12. Linear regression between monthly Newfoundland encrusting *C. compactum* Mg/Ca (8 transects averaged from 4 samples), *L. glaciale* rhodolith Mg/Ca (12 transects averaged from 4 samples) and Reynolds temperature over 18 years.

Figure 13. Monthly Newfoundland encrusting *C. compactum* (8 transects averaged from 4 samples) and *L. glaciale* rhodolith (12 transects averaged from 4 samples) Mg/Ca time series (top) compared to monthly instrumental temperatures (bottom). A seawater temperature of -1.94°C is assigned to periods of ice cover in MODIS data.

Figure 14. Newfoundland encrusting *C.* and *L. glaciale* rhodolith annual Mg/Ca time series compared to annual instrumental temperatures. Reynolds SST correlated with encrusting *C. compactum* ($n=18$, $r=0.37$, $p=0.06$), and *L. glaciale* ($n=18$, $r=0.37$, $p=0.06$).

Figure 15. Model of rhodolith growth; internal lines represents annual growth increments. Left: Increments are wider on top where there is more available light. Right: Same rhodolith two years after being turned, with wider growth bands forming on top of the area with narrower growth increments previously orientated to the bottom and vice versa. Note: this is a (representation) sketch, not based on data.

Tables

Table 1: Summary of correlations:

Intra-sample monthly (average of multiple linear regressions for each morphology)	Correlation r(p)
Encrusting <i>C. compactum</i> (Greenland)	0.34 (<0.001)
Rhodolith <i>C. compactum</i> (Greenland)	0.33 (<0.001)
Rhodolith <i>L. glaciale</i> (Greenland)	0.43 (<0.001)
Encrusting <i>C. compactum</i> (Newfoundland)	0.61 (<0.001)
Rhodolith <i>L. glaciale</i> (Newfoundland)	0.43 (<0.001)
Inter-sample monthly (multiple linear regression; 2-3 transects/specimen averaged then compared within morphology)	Correlation r(p)
Encrusting <i>C. compactum</i> (Greenland)	0.55 (<0.001)
Rhodolith <i>C. compactum</i> (Greenland)	0.64 (<0.001)
Rhodolith <i>L. glaciale</i> (Greenland)	0.63 (<0.001)
Encrusting <i>C. compactum</i> (Newfoundland)	0.61 (<0.001)
Rhodolith <i>L. glaciale</i> (Newfoundland)	0.73 (<0.001)
Correlation with local monthly Reynolds SST (18 years) all transects and specimens averaged	Correlation r(p)
Encrusting <i>C. compactum</i> (Greenland)	0.64 (<0.001)
Rhodolith <i>C. compactum</i> (Greenland)	0.62 (<0.001)
Rhodolith <i>L. glaciale</i> (Greenland)	0.58 (<0.001)
Encrusting <i>C. compactum</i> (Newfoundland)	0.85 (<0.001)
Rhodolith <i>L. glaciale</i> (Newfoundland)	0.84 (<0.001)
Correlations of annually averaged Mg/Ca with local seasonal (March-Aug) Reynolds SST (18 years)	Correlation r(p)
Encrusting <i>C. compactum</i> (Greenland)	0.35 (0.077)
Rhodolith <i>C. compactum</i> (Greenland)	-0.31 (0.11)
Rhodolith <i>L. glaciale</i> (Greenland)	-0.04 (0.44)
Encrusting <i>C. compactum</i> (Newfoundland)	0.37 (0.065)
Rhodolith <i>L. glaciale</i> (Newfoundland)	0.37 (0.065)

Table 2. Individual Newfoundland specimen (annual average) correlations with seasonal (Mar-Aug) annual Reynolds SST.

Encrusting <i>C. compactum</i>	Correlation r(p)
08-SJ-21	0.43 (0.04)
08-SJ-28	0.19 (0.23)
08-SJ-02	0.28 (0.13)
08-SJ-03	-0.005 (0.49)
Rhodolith <i>L. glaciale</i>	Correlation r(p)
08-SJ-RH01	0.25 (0.16)
08-SJ-RH02	0.27 (0.15)
08-SJ-RH03	-0.05 (0.42)
08-SJ-RH04	0.06 (0.41)

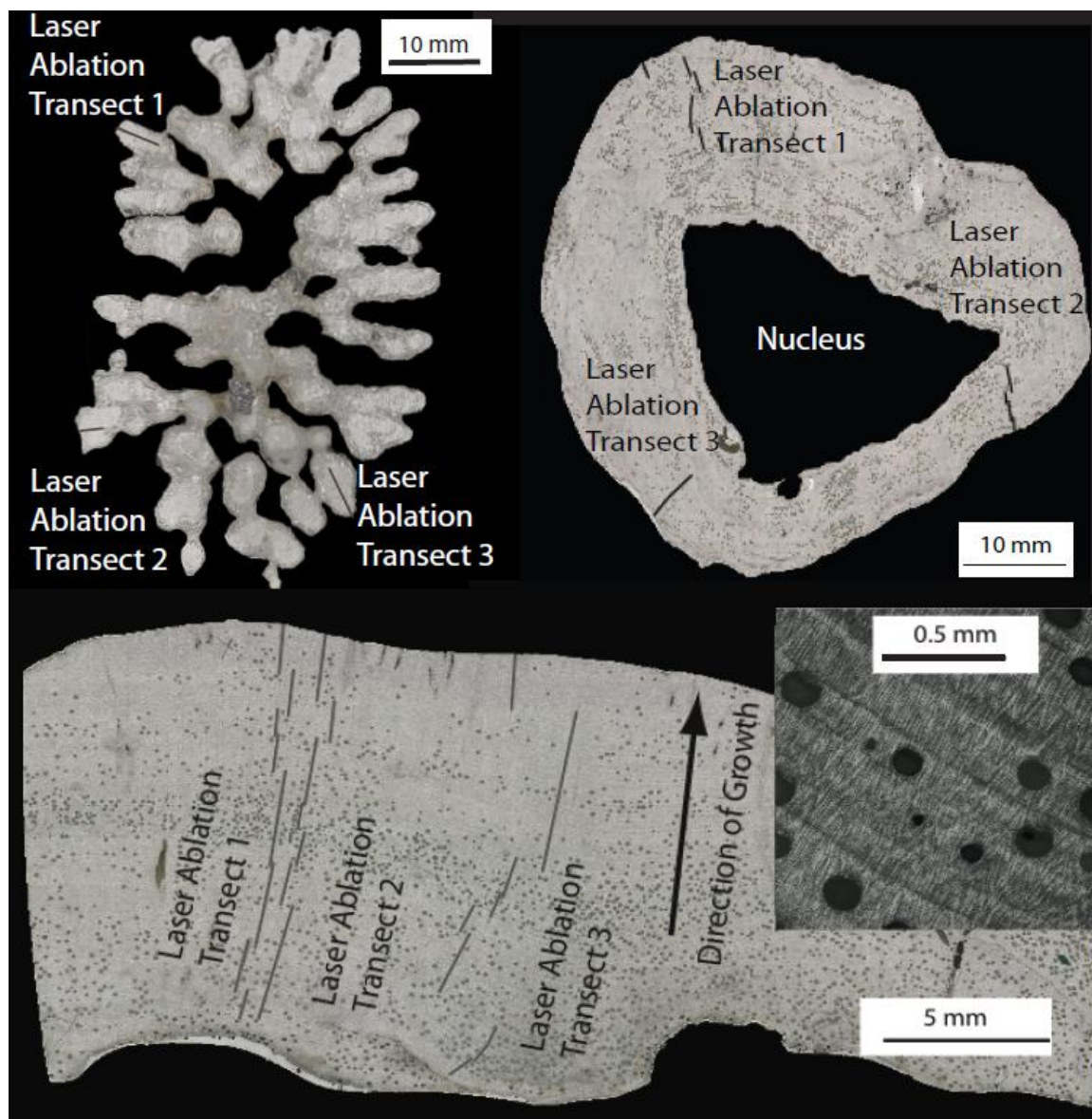


Fig. 1

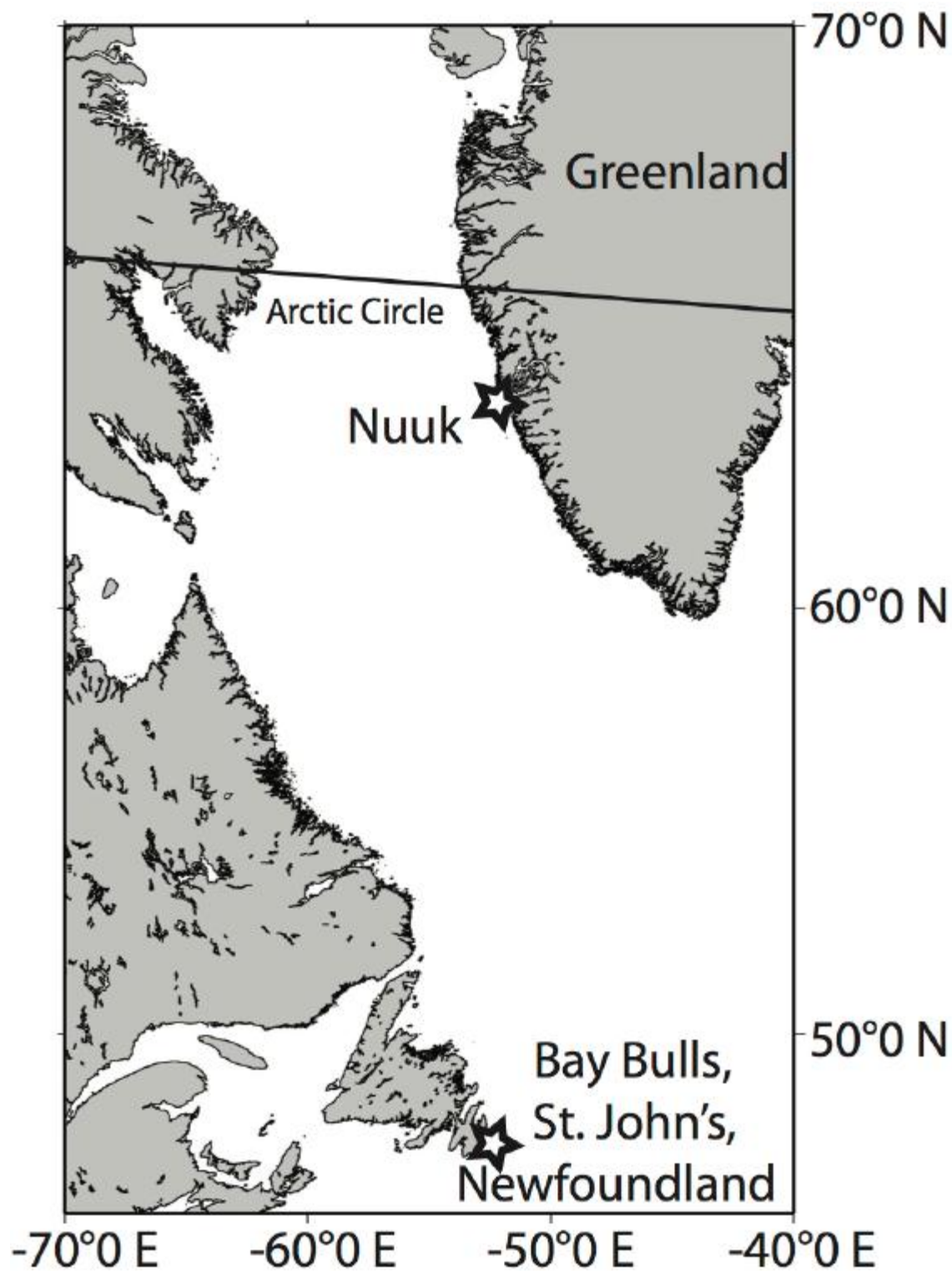


Fig. 2

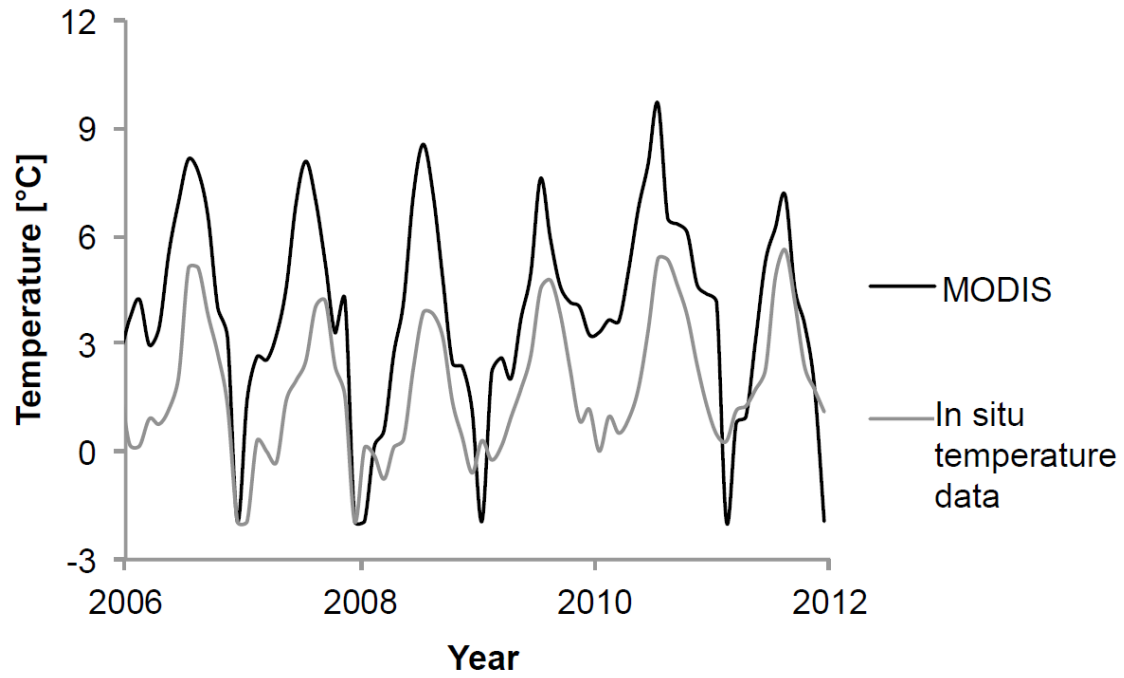


Fig. 3

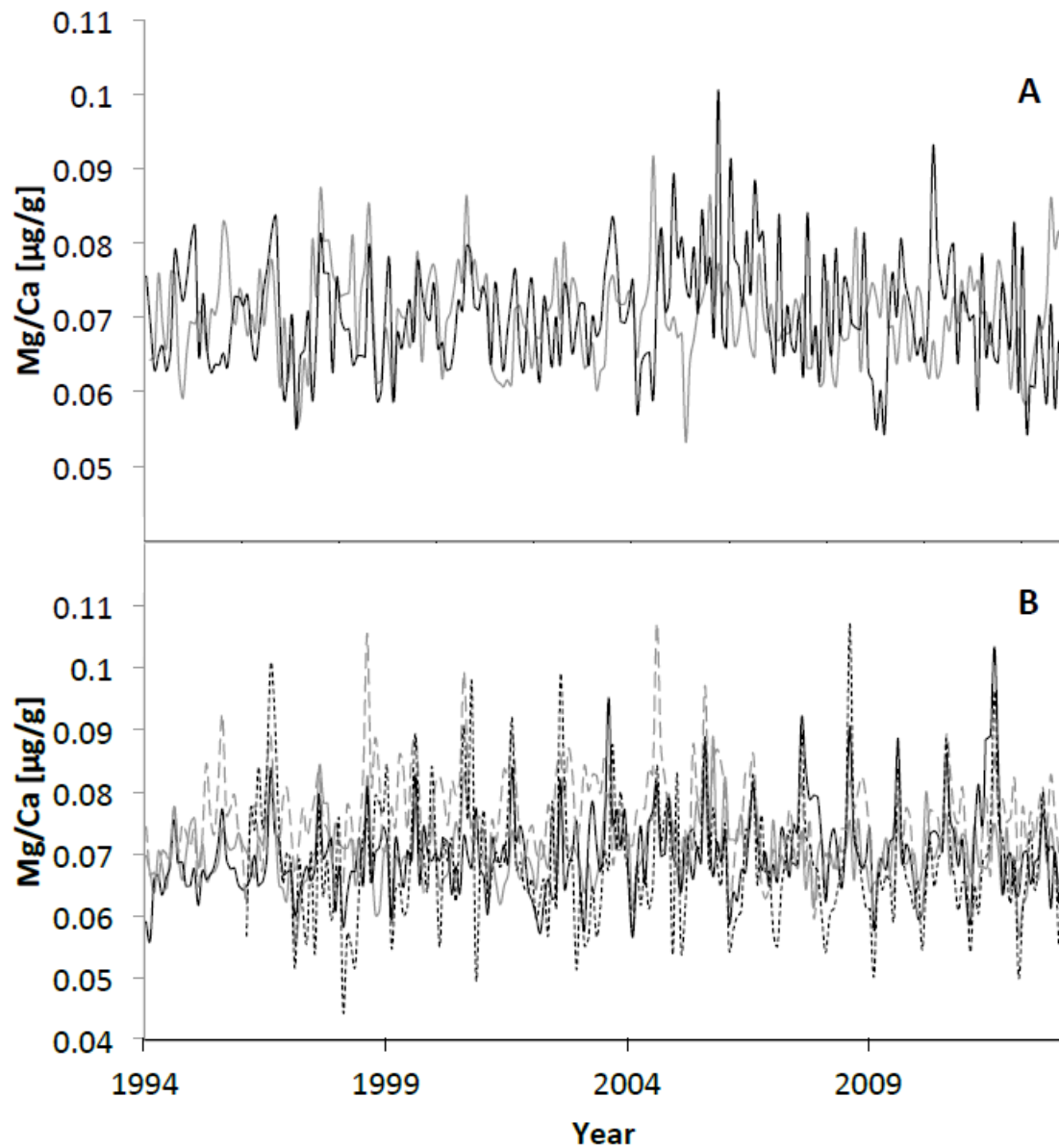


Fig. 4

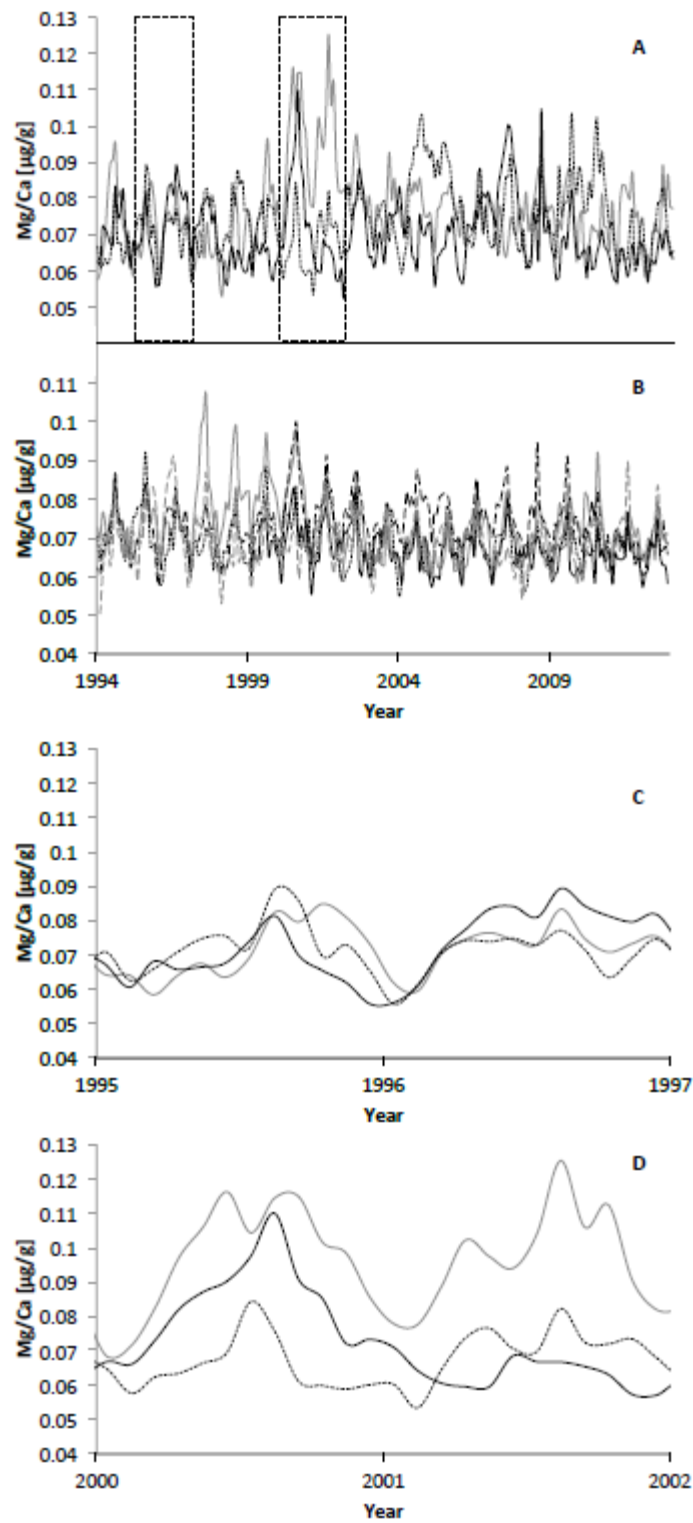


Fig. 5

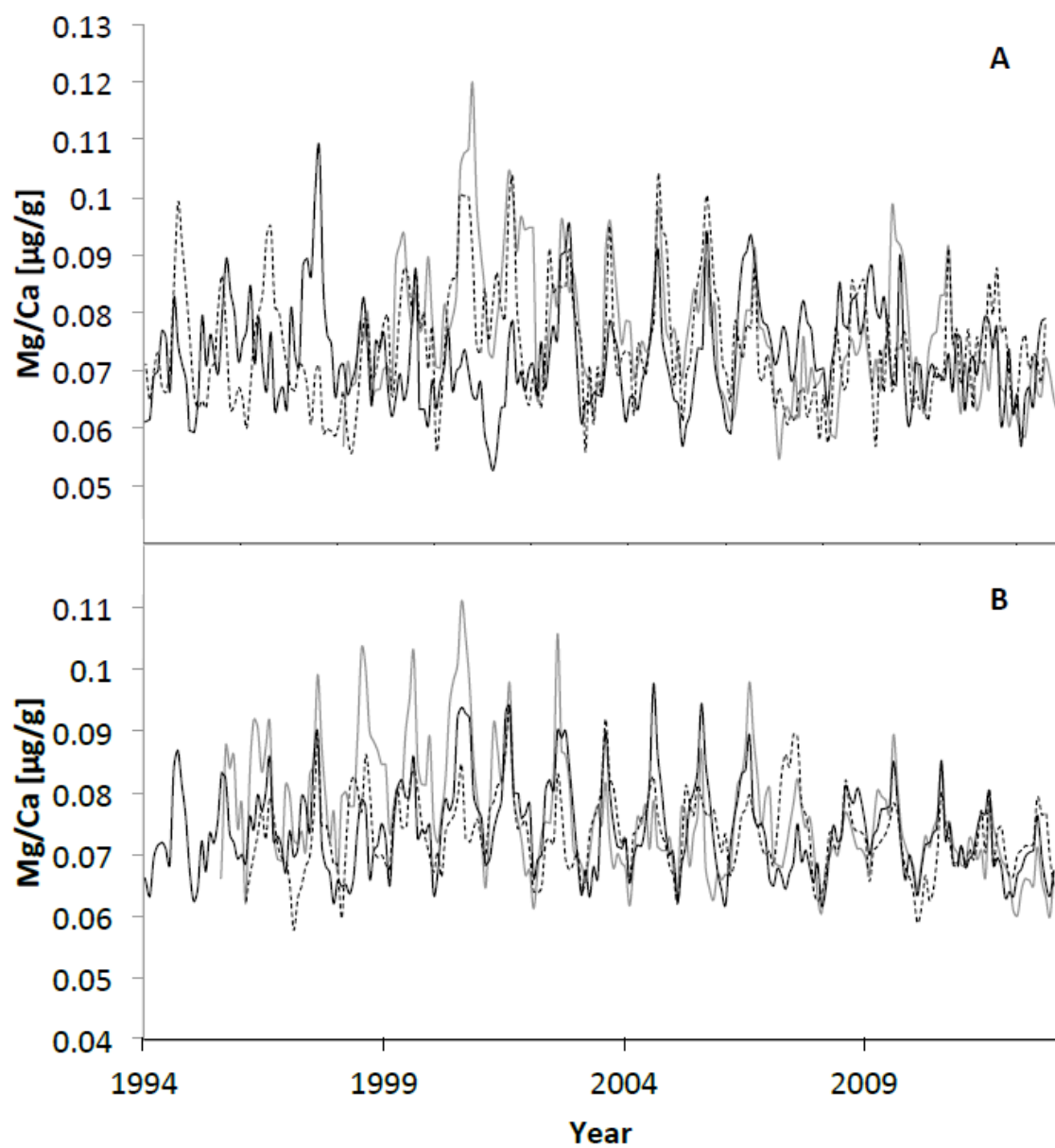


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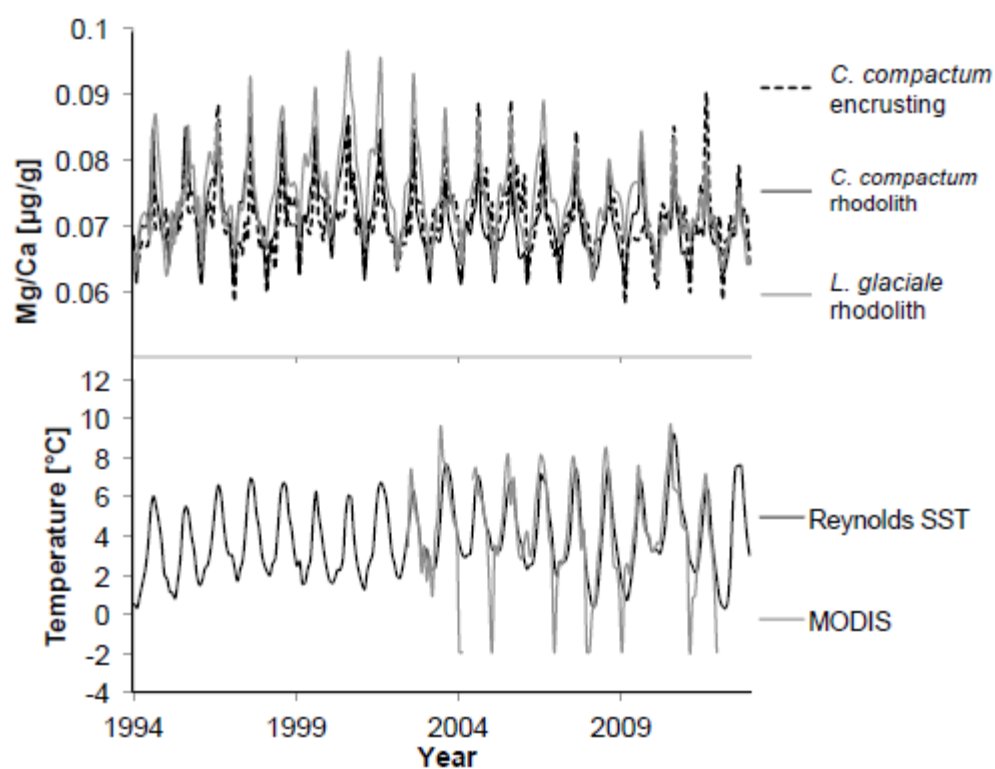


Fig. 7

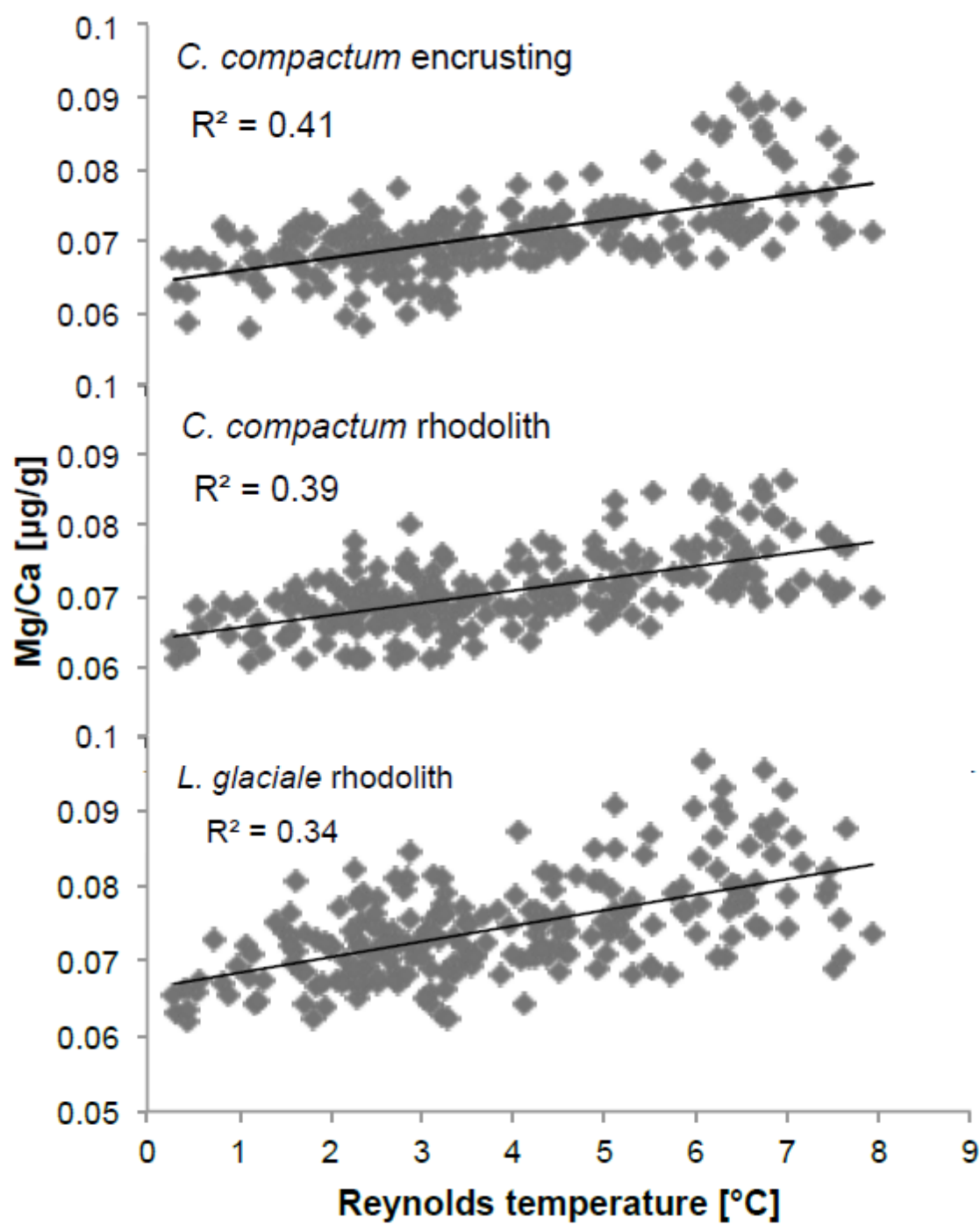


Fig. 8

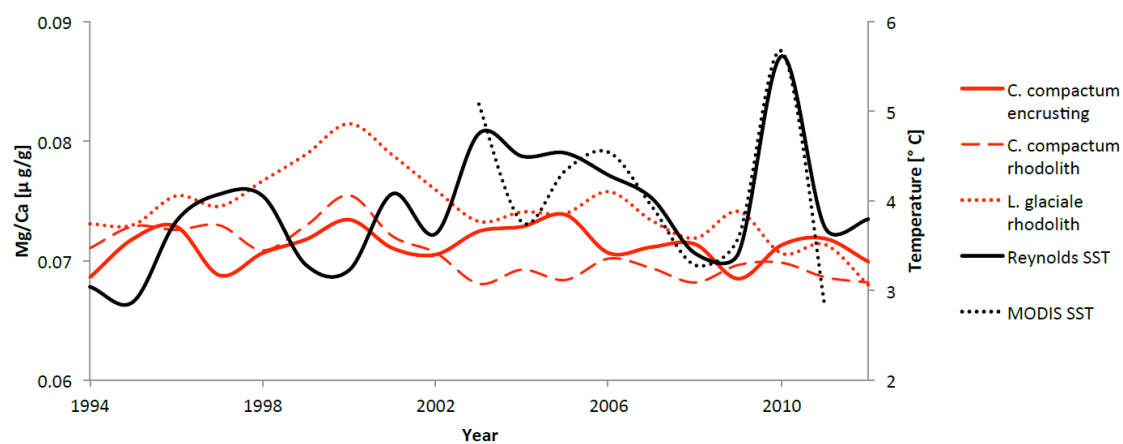


Fig. 9

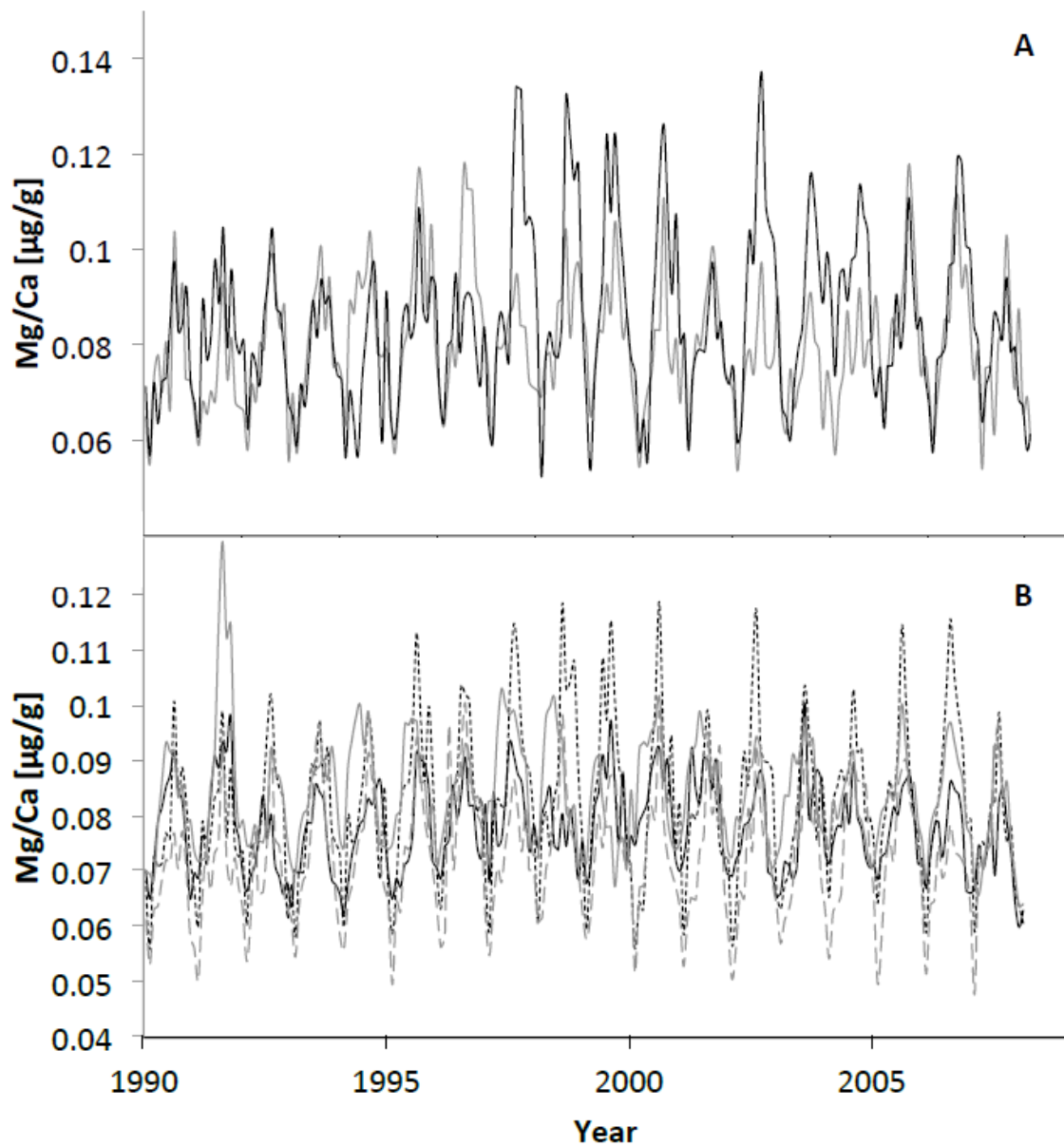


Fig. 10

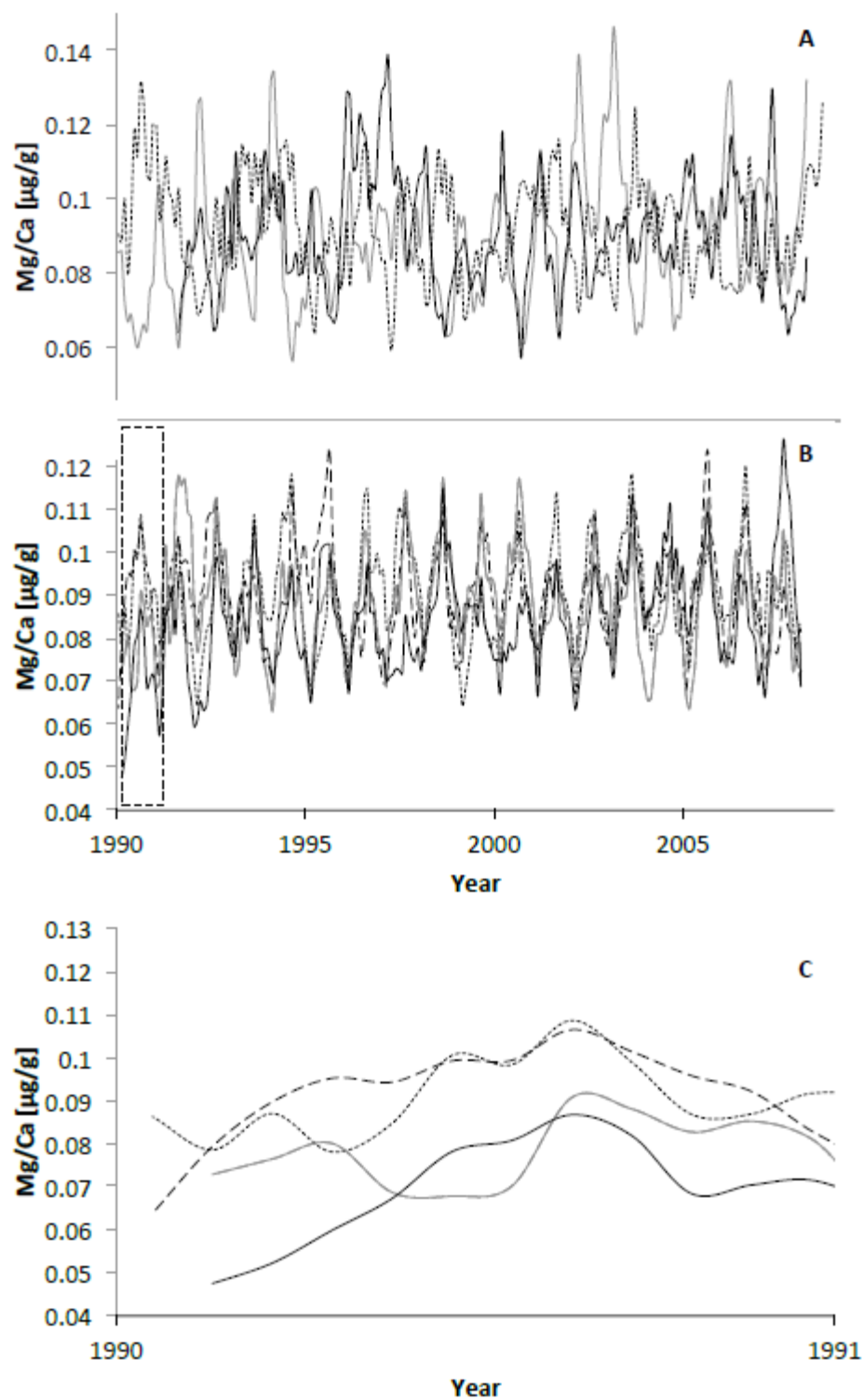


Fig. 11

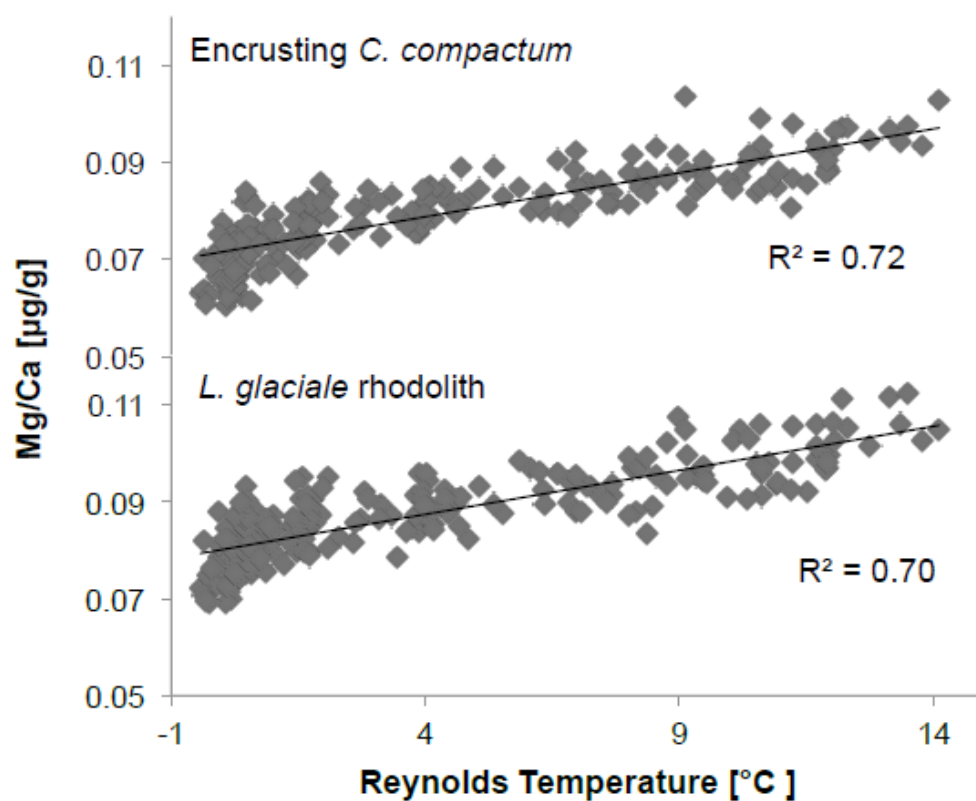


Fig. 12

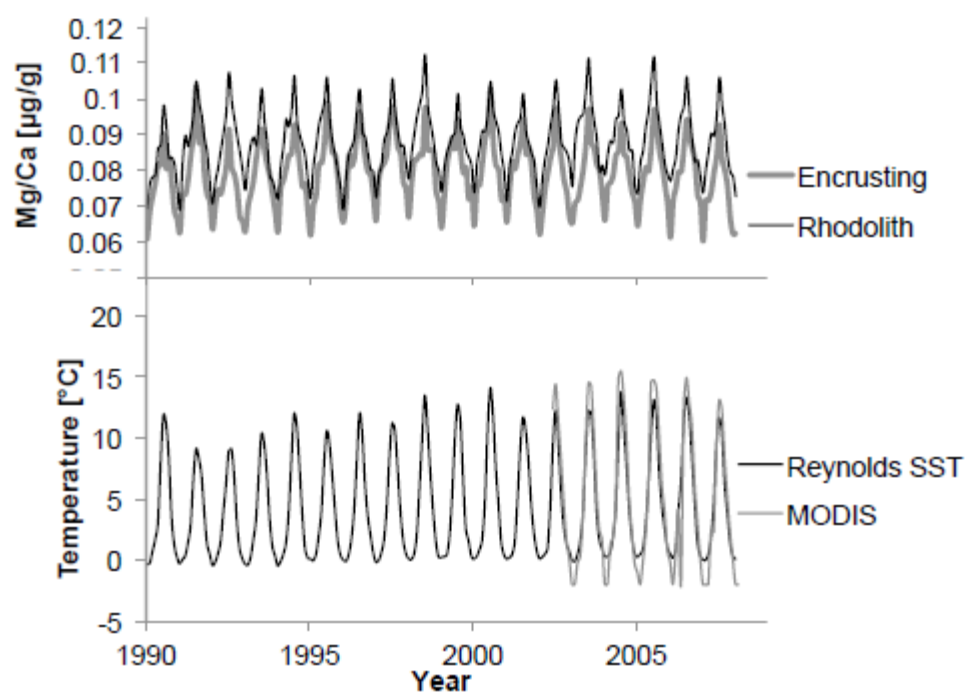


Fig. 13

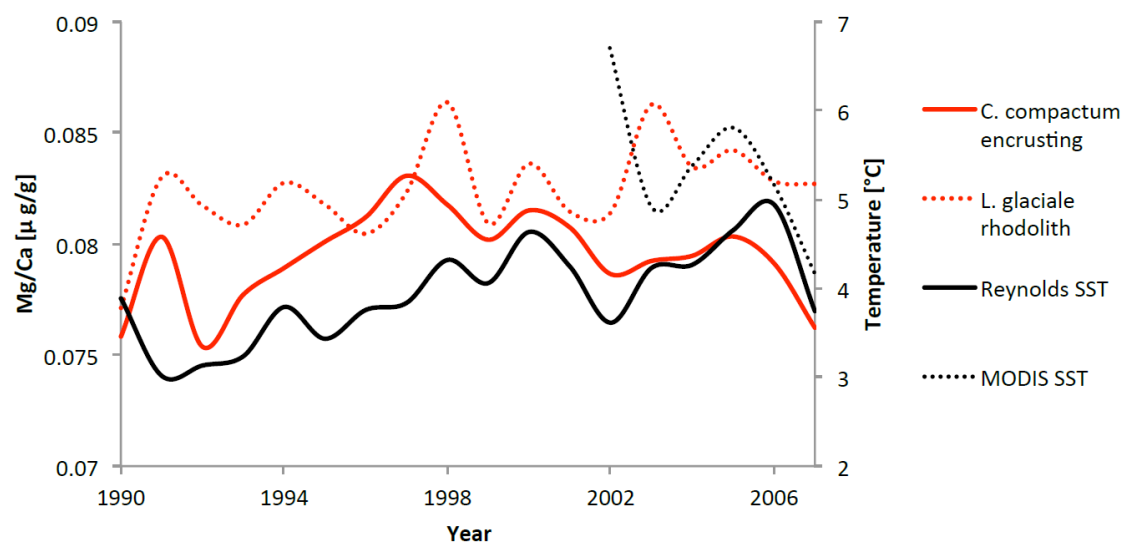


Fig. 14

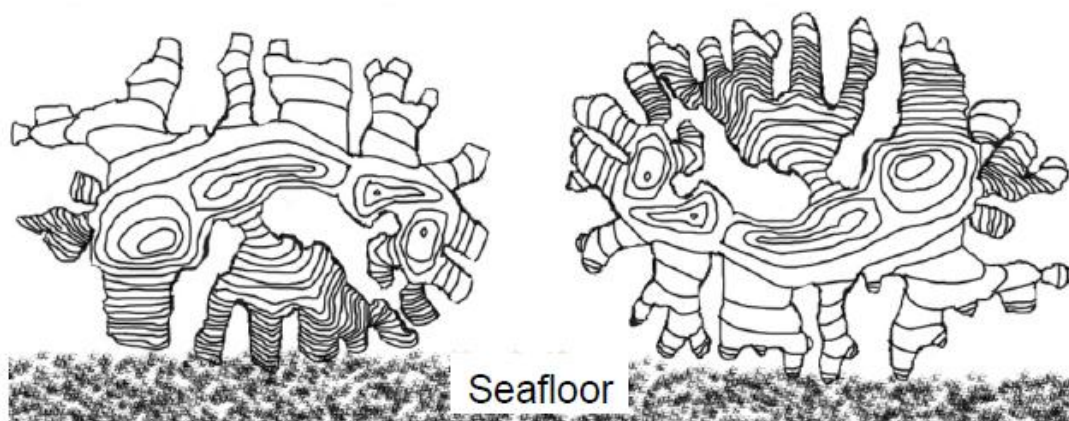


Fig. 15